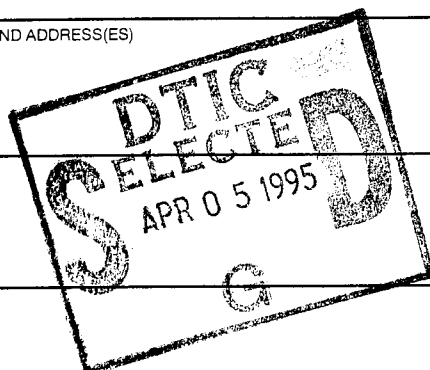


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Corpus Callosum Size in Delphinid Cetaceans

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Abstract

The midsagittal surface area of the corpus callosum was determined by computer-assisted morphometry in juvenile and adult members of 13 species of the cetacean family Delphinidae. In 57 brains, absolute callosal areas ranged from 104 to 829 mm². When compared to other mammal groups possessing a corpus callosum, callosal area in dolphins was smaller in relation to brain mass with a ratio range (mm²/g) of 0.08–0.31. The corpus callosum was decreased relative to brain mass in the larger-brained odontocetes, suggesting that increases in brain size were not necessarily allied with needs for equivalent increases in callosal linkage. One delphinid species, *Tursiops truncatus*, for which the largest single-species sample was available, was examined for sex differences in callosal size relative to brain mass. Among 10 males and 5 females the averaged ratio was not distinguishable between sexes.

Introduction

Although descriptions and functional considerations of the corpus callosum can be found in the early literature of brain anatomy [Mall, 1909; Cameron, 1917; Suitsu, 1920/1921], it was largely the more recent work of Myers and Sperry and their associates that redirected attention to this structure. These workers in the 1950's and 60's presented evidence that the corpus callosum is involved in the communication and coordination between the cerebral hemispheres, particularly in the context of cerebral lateralization in humans [Myers and Sperry, 1953; Myers, 1956, 1959; Sperry, 1961, 1962; Gazzaniga, 1966; Bogen 1969].

Recently, many investigators have examined the midsagittal area of the corpus callosum, both quantitatively and qualitatively, as an index of potential callosal variations relative to sex, handedness, age, brain mass and/or functional asymmetries in humans and other primates [Baack et

al., 1982; de Lacoste-Utamsing and Holloway, 1982; Demeter et al., 1985; Malobabic et al., 1985; Witelson, 1985, 1986; Bleier et al., 1986; Holloway and de Lacoste, 1986; Nasrallah et al., 1986; Weber and Weis, 1986; Yoshi et al., 1986; Kertesz et al., 1987; de Lacoste and Woodward, 1988; Peters, 1988; Demeter et al., 1988; O'Kusky et al., 1988; Hayakawa et al., 1989].

Comparatively few studies have followed the phylogenetic approach of Anthony [1938], however, in considering variations in corpus callosum development through a broad range of species. Anthony examined midsagittal callosal area relations in 26 mammalian species where brain size ranged from 22 g (lemur) to 4,460 g (elephant). Although each species in his collection was represented by only a single individual, he reported the smallest callosal area relative to brain mass in his only cetacean representative, the common dolphin, *Delphinus delphis*, a member of the family Delphinidae in the toothed whale (odontocete)

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Fig. 1. Photograph of the 1,609 g brain of *T. truncatus* Tt20F cut in midsagittal section to expose the corpus callosum for measurement. The area measured is outlined by dashed lines in the inserted photograph.

suborder of cetaceans (whales, dolphins, porpoises). Nieto et al. [1976] also compared the midsagittal area of the corpus callosum with brain mass across several species, including a single individual pantropical spotted dolphin, *Stenella graffmani* (now revised to *S. attenuata*), which they emphasized had a very small corpus callosum relative to brain mass. Ridgway [1986] also noted the small size of the cetacean corpus callosum relative to brain mass when compared to other mammals. An illustration in his study compared the midsagittal sections from the brain of a killer whale, *Orcinus orca*, and the brain of a human: it was noted that, while the killer whale brain was five times larger than that of the human, the corpus callosum cross-sectional areas of both appeared similar. Previous examinations of callosal midsagittal area in cetaceans each involved only a single individual. In this study we have sought to enlarge the evidence addressing the size of the corpus callosum in cetaceans by examining its relation to the size of the brain in 13 species of the cetacean family Delphinidae.

Materials and Methods

Whole brains were collected from 57 juvenile and adult delphinid odontocete (toothed) cetaceans, representing 13 species. Some specimens were collected at necropsy from animals that died of natural causes in our laboratory, in other laboratories, or in marine parks during the past twenty years. Some other specimens were from cetaceans that beached themselves (strandings or die-offs) and still others were from animals captured incidental to commercial fishing and made available to us by the U.S. National Marine Fisheries Service. Most brains were immersion-fixed in formalin and held for varying periods (months to years) prior to the preparation and examination of callosal midsagittal areas. Brain mass (BM) measurements used for correlations generally represent the fresh state; however, for several brains, mass could only be determined after varying periods in fixative. Since shrinkage artifact can be assumed to have an effect on BM and corpus callosum measurements, we examined the amount of shrinkage in 19 delphinid brains that had been comparatively weighed over time. Losses in mass ranged from 1.6–7.8%. We considered the impact of 7.8% loss on our data, as the worst case scenario, but found no indication that the conclusions of our study would be altered.

The midsagittal area of the corpus callosum (CCA) was exposed by longitudinal midline section and was photographed with a centimeter scale positioned in the same plane (fig. 1.). Callosal area was

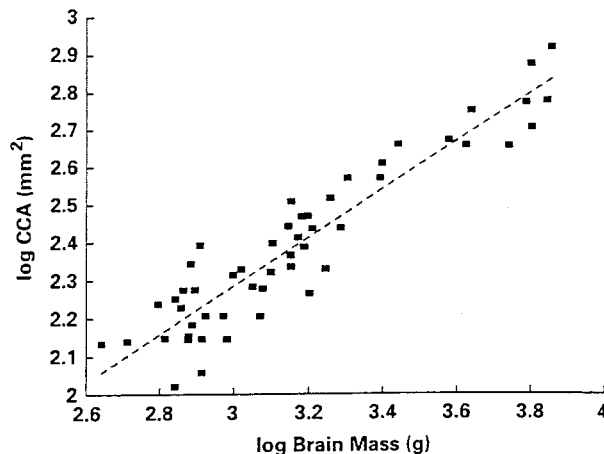


Fig. 2. A plot of log values in 57 delphinids demonstrates an increase in midsagittal corpus callosum area (CCA) as brain mass (BM) increases ($\log y = 0.364 + 0.64 \log x$, $p < 0.01$, $r = 0.93$), but shows that CCA enlargement declines relative to BM as BM expands.

determined by tracing the callosal perimeter on the photograph with a computer-based morphometry digitizing system (Bioquant System IV®). Three measurements were made of each image and the mean was determined as the final value.

Individual animals were maturity-indexed as juvenile, adult or old adult. Except where we had personal knowledge of an animal's maturity, these assessments were estimated on the basis of body length as interpreted from the published literature [Sergeant et al., 1973; Klinowska, 1991].

Selected published [Wilson, 1933; Pilleri, 1974] and unpublished photographs of midsagittal callosal sections were also examined to permit comparisons with more rarely collected cetaceans, including the minke whale, *Balaenoptera acutorostrata*, the blue whale, *Balaenoptera musculus*, and the Ganges river dolphin, *Platanista gangetica*. A limited sample of callosa from other marine mammal species, including the California sea lion, *Zalophus californianus* (4), the walrus, *Odobenus rosmarus* (1), and the West Indian manatee, *Trichechus manatus* (1), was photographed and measured for additional comparison.

The original research reported here was conducted in accordance with guidelines promulgated under the U.S. Marine Mammal Protection Act and the Animal Welfare Act.

Results

Body mass in our study animals ranged well over two orders of magnitude, from approximately 30 kg to just over 5,500 kg. Brain mass ranged from 435 g to 7,100 g (table 1). Absolute midsagittal area of the corpus callosum for 57 individual marine delphinids ranged from 104.1 mm² in an adult female common dolphin, *D. delphis* (Dd#7) to 828.6

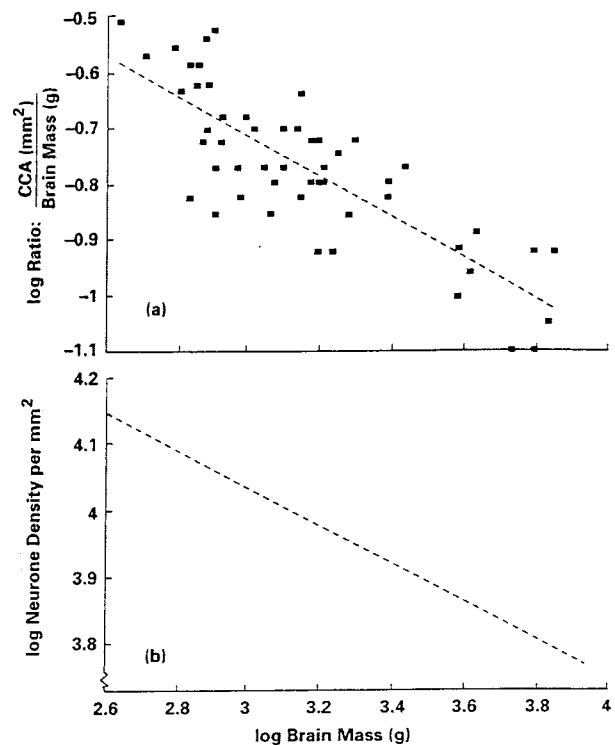


Fig. 3. Tower (1954) maintained that isocortical neuron density (he used the term neurone) decreased in mammals with larger brains. The extended slope of his regression line (-0.32 , $p < 0.001$, $r = -0.99$) of neuron density (b) relative to increasing brain size through the brain size range equivalent to the brains in our study (a) is similar to the decline in the size of the corpus callosum area relative to brain mass with increasing brain size in our 57 delphinids ($\log y = 0.386 - 0.366 \log x$, $p < 0.01$, $r = -0.83$).

mm² in an old adult male killer whale, *O. orca* (SW88142) (table 1). The CCA increased with BM, and the ratio of CCA to BM in grams for all individuals varied from 0.079 to 0.310 (fig. 2, table 1). Averaged by species, the ratio ranged between 0.097 (*O. orca*) and 0.272 (*Stenella longirostris*) (table 2). In our sample, overall, larger-brained species possessed smaller CCA relative to BM (fig. 3, table 2). Thus *O. orca*, with the largest absolute adult brain mass in our collection presented the smallest mean CCA/BM (0.097), whereas *S. longirostris*, which has the smallest absolute adult brain mass, yielded the largest mean ratio (0.272). Sexual dichotomy in CCA/BM values was difficult to assess because sample sizes were generally not large enough to test for significant differences. The largest numbers of individuals within a single species were available for the Atlantic bottlenose, dolphin, *Tursiops truncatus*,

Table 1. Brain and body morphometrics

Species/code #	Age index ^a	Body length (cm)	Body mass (kg)	Brain mass (g)	CC area (mm ²)	CCA/BM ratio
Order Odontoceti, family Delphinidae						
<i>Cephalorhynchus commersonii</i> (3)						
Females						
SWCc8329	a	147	42	833	160.2	0.192
Cc91032	a	157	48	725	186.2	0.257
Males						
SWCc9088	a	150	41	685	176.8	0.258
<i>Delphinus delphis</i> (7)						
Females						
(Dd)SW0883	j	137	34	714	167.9	0.235
P76024	a	215	86	809	138.9	0.172
Dd110879	a	170	55	688	104.1	0.151
SW910723	a	188	69	749	139.5	0.186
Males						
Dd8448B	j	155	46	810	113.4	0.140
Dd8436B	a	191	81	620	171.9	0.277
Dd486M	a	195	91	757	218.9	0.289
<i>Feresa attenuata</i> (4)						
Males						
C811	j	199	110	1,040	211.6	0.203
C803	j	190	—	987	206.2	0.209
C815	j	208	140	1,252	208.0	0.166
Unknown Sex						
SW8264B	?	—	—	841	175.1	0.208
<i>Globicephala macrorhynchus</i> (3)						
Females						
KwGm0791	a	313	386 ^b	2,466	405.3	0.164
Males						
Gm910412	a	420	—	2,449	369.2	0.151
Gm910413	a	430	—	2,733	456.6	0.167
<i>Grampus griseus</i> (2)						
Females						
Gg9103	j	250	159	1,991	370.5	0.186
Gg766F	o	288	282	1,738	212.2	0.122
<i>Lissodelphis borealis</i> (1)						
Females						
SWLb2	a	204	73	1,162	160.0	0.138
<i>Lagenorhynchus obliquidens</i> (3)						
Females						
SW84189	a	189	105	1,182	188.3	0.159
SW86051	a	220	130	1,253	248.0	0.198
Males						
Lo#1	j	158	46	931	159.2	0.171
<i>Orcinus orca</i> (6)						
Females						
SW1077	a	582	2,409	6,215	742.1	0.119
SW89079	a	536	2,090	5,667	446.7	0.079
SWTX0951	a	516	2,077	6,299	507.1	0.081
Males						
SW0683	o	618	2,677	6,052	593.1	0.098
Oo8701	o	675	5,568	6,875	596.4	0.087
SW88142	o	665	3,455	7,100	828.6	0.117

(Table 1 continued on next page.)

Table 1 (continued)

Species/code #	Age index ^a	Body length (cm)	Body mass (kg)	Brain mass (g)	CC area (mm ²)	CCA/BM ratio
<i>Pseudorca crassidens</i> (4)						
Females						
PS0487F	j	329	310	4,307	559.8	0.130
SWPc8729	a	379	536	4,739	462.5	0.098
SWPc8329	a	359	385	4,150	451.3	0.109
Males						
Pc739M	j	325	377	3,798	461.4	0.122
<i>Stenella attenuata</i> (4)						
Males						
SWF289	a	213	—	805	245.5	0.305
SWF789	a	198	—	641	140.6	0.219
SWF489	a	180	—	748	142.4	0.190
SWF589	a	191	—	765	151.1	0.198
<i>Stenella longirostris</i> (3)						
Females						
SWF1189	j	150	—	435	134.8	0.310
SWF389	a	185	—	514	136.5	0.266
Males						
SWF1289	a	160	—	775	185.6	0.239
<i>Steno bredanensis</i> (2)						
Females						
Sb910525	a	228	91 ^b	1,503	243.0	0.162
Males						
MM9119	a	213	91 ^b	1,575	182.6	0.116
<i>Tursiops truncatus</i> (15)						
Females						
Tt663F	j	214	131	1,404	214.1	0.152
Tt654F	j	226	126	1,388	233.9	0.169
1B7154	a	242	226	1,410	319.7	0.227
Tt453F	o	227	140	1,112	191.1	0.172
Tt20F	o	252	197	1,609	258.1	0.160
Males						
TtGF9189	j	144	43	954	139.3	0.146
Tt024M	a	234	158	1,382	274.5	0.199
Tt743M	a	237	135	1,562	256.8	0.164
Tt9006B	a	241	—	1,590	255.8	0.161
Tt665M	j	242	136	1,487	252.7	0.170
Tg90522	o	253	245	1,910	272.6	0.143
Tt87012	a	259	186	1,630	269.2	0.165
SWTt0587	o	260	190	1,509	291.3	0.193
Tg624M	a	281	222	1,828	324.9	0.178
MML9014	o	295	193	1,563	291.4	0.186

^a Age index: j = juvenile; a = adult; o = old adult.

^b Estimated body mass.

where CCA/BM was determined in brains from 5 females and 10 males and examined for sex difference (table 1). No statistical difference in the ratio existed between sexes (0.17 in males and 0.18 in females) at $p = 0.7226$. Although BM is generally similar in male and female *Tursiops*, mean

BM in our CCA sample of this species was larger in males (1,542 g) than in females (1,385 g); accordingly, the statistical indistinguishability of CCA/BM between sexes was maintained by a proportionately similar dichotomy in CCA (262.9 mm² in males and 243.4 mm² in females) (table 1).

Table 2. Odontocete corpus callosum area (mm²) to brain mass (g) ratio ranges and means and brain mass means by species for juveniles and adults, sorted within families by ascending species mean ratio

Species	n	Range	Mean	Brain mass (g mean)
Delphinidae				
<i>Orcinus orca</i>	6	0.079–0.119	0.097	6,368
<i>Pseudorca crassidens</i>	4	0.098–0.130	0.115	4,249
<i>Lissodelphis borealis</i>	1	0.138	0.138	1,162
<i>Steno bredanensis</i>	2	0.116–0.162	0.139	1,539
<i>Grampus griseus</i>	2	0.122–0.186	0.154	1,865
<i>Globicephala macrorhynchus</i>	3	0.151–0.167	0.161	2,549
<i>Tursiops truncatus</i>	15	0.143–0.227	0.172	1,489
<i>Lagenorhynchus obliquidens</i>	3	0.159–0.198	0.176	1,122
<i>Feresa attenuata</i>	4	0.166–0.209	0.197	1,030
<i>Delphinus delphis</i>	7	0.140–0.289	0.207	735
<i>Stenella attenuata</i>	4	0.190–0.305	0.228	740
<i>Cephalorhynchus commersonii</i>	3	0.192–0.258	0.236	748
<i>Stenella longirostris</i>	3	0.239–0.310	0.272	575
Kogiidae				
<i>Kogia breviceps</i>	5	0.15–0.23	0.189	768
<i>Kogia simus</i>	1	0.23	0.230	625
Monodontidae				
<i>Delphinapterus leucas</i>	6	0.13–0.21	0.147	2,009
Physeteridae				
<i>Physeter macrocephalus</i>	1 ^a	0.17	0.174	3,784
Ziphiidae				
<i>Mesoplodon europaeus</i>	1	0.24	0.238	971

^a Neonate.

We compared our linear regression describing the inverse relationship between CCA/BM and brain mass (fig. 3) with the regression line of Tower (1954) who related neuron density and brain mass. We picked five points on Tower's regression line representing brain masses of 400 to 8,000 g, a span that encompassed the range of brain sizes in our study. This segment of Tower's regression is compared with our regression of CCA/BM and brain mass (fig. 3).

We also made preliminary CCA measurements in four other odontocete genera representing five species (table 2). As for our delphinids, the ratio CCA/BM was small relative to that in most mammals, with all ratios encompassed by the range of the delphinid sample and family means or single values of 0.210 (Kogiidae), 0.147 (Monodontidae), 0.174 (Physeteridae) and 0.238 (Ziphiidae).

The brain of the Ganges river dolphin, *P. gangetica*, figured in Pilleri (1974) had a CCA of 126.3 mm² (table 3). The small brain size (293 g) of this freshwater dolphin resulted in a comparatively high CCA/BM of 0.43. In both our minke whale, *B. acutorostrata*, and Wilson's (1933) blue whale, *B. musculus*, we calculated a CCA/BM of 0.15 (table 3). In four juvenile California sea lions, *Z. californianus*, CCA ranged from 109.2 to 222.2 mm², giving a

CCA/BM range of 0.348 to 0.529 (mean, 0.442). In a single walrus, *O. rosmarus*, brain we measured CCA as 188.7 mm² with a CCA/BM of 0.151. The highest ratio of our sample (0.829) occurred in a West Indian manatee, *T. manatus*, where CCA was 250.3 mm² and brain mass was 302.0 g (table 3).

Discussion

Phylogenetic comparisons of corpus callosum size (defined by its area in midsagittal section) in relation to brain mass have been rarely reported. However, our findings provide quantitative support for the suggestion that the corpus callosum is small relative to brain mass in the cetacean order. Anthony [1938] examined this feature in 26 mammalian species, each represented by a single individual, and determined ratios of corpus callosum area to brain mass, expressed in mm²/g, ranging from 0.105 to 1.125. In only three brains from his sample did the ratio fall below the highest value (0.310) in our collection of 57 delphinids; these consisted of a common dolphin (0.105), an Indian elephant (0.181) and a monk seal (0.293). While our ratio for

Table 3. Brain morphometrics in other marine mammal species

Species (n#)/code #	Brain mass (g)	CC area (mm ²)	CCA/BM ratio (mm ³ /g)
Cetacea			
Mysticeti			
<i>B. acutorostrata</i> (1)			
Males			
BA9010B	2,217	334.8	0.151
<i>B. musculus</i> (1)			
Unknown sex			
Bm001	5,678	850.1	0.150
Odontoceti			
<i>P. gangetica</i> (1)			
Females			
Pg464	293	126.3	0.431
Carnivora			
<i>Z. californianus</i> (4)			
Females			
Zc559F	314	109.2	0.348
Zc001	327	138.1	0.422
Males			
Zc002	420	222.2	0.529
Unknown sex			
Zc003	372	173.8	0.467
<i>Q. rosmarus</i> (1)			
Females			
SW89047	1,250	188.7	0.151
Sirenia			
<i>T. manatus</i> (1)			
Unknown sex			
Tm8869B	302	250.3	0.829

the common dolphin, based on a larger sample ($n = 7$) was higher than Anthony's with a mean of 0.207 (range, 0.140–0.289), it is notable that Anthony's lowest ratio through a broad range of mammal species occurred in his only cetacean representative. In a more recent study involving 14 mammal species (also limited to observations in single individuals for each species) Nieto et al. [1976] provided data that generated ratios ranging from 0.217 through 3.840. Although the brains in his sample were weighed with the cerebellum removed, thereby artifactually raising the ratio, it is still significant that the single cetacean (a pantropical spotted dolphin) in his study, as in that of Anthony, possessed the smallest corpus callosum relative to brain mass. Ridgway [1986] called attention to the reduced corpus callosum of cetaceans, noting that callosal midsagittal size appeared similar in single brains of a human and a killer whale, even though brain mass in the whale was some five times that of the human. All three cetaceans (common

dolphin, pantropical spotted dolphin and killer whale) considered by the previous authors come from the delphinid family of odontocetes (toothed whales), as did our 57 brains representing 13 species. Our measurement of the corpus callosum from a midsagittal photograph [in Pilleri, 1974] of the brain of a single Ganges river dolphin (family Platanistidae, the most primitive cetacean family from an evolutionary perspective), and our calculation of the ratio (0.431) based on the brain mass given in Pilleri's article, suggest a comparatively large corpus callosum in this cetacean family (which also has the smallest brain mass among cetacean families). However, our preliminary observations of corpus callosum size from small samples in four other odontocete families (Kogiidae, Monodontidae, Physeteridae and Ziphiidae), as well as in two single individuals of mysticete (baleen) whales from two species of the family Balaenopteridae, suggest that a relative reduction in corpus callosum size at the brain midline may be the prevailing theme of the cetacean order. We have made casual observations of our study specimens regarding the presence of other cerebral commissures and have thus far found no indication that the relative reduction of the cetacean corpus callosum has been compensated by an enlargement of other commissural tracts, such as has been documented in marsupials where the corpus callosum is absent and the anterior commissure is the primary cerebral link [Ebner, 1967].

Despite this reduction in the corpus callosum in cetaceans, it is apparent that callosal size relative to brain mass in our 57 delphinids is not a fixed relationship since the ratios occur through a broad range of values (0.079–0.310). Our data indicate that this range of ratios varies at least in part with brain mass itself, with the size of the corpus callosum decreasing relative to increasing brain mass. Such an explanation is compatible with the rather large ratio (0.431) we determined for the single Ganges river dolphin whose brain mass (293 g) is among the smallest within the cetacean order. The inverse relation between the CCA/BM and BM appears further upheld by our initial, though limited, observations in other marine mammal taxa (table 3). In four juvenile California sea lions, where brain mass ranged from 314 to 420 g, callosal to brain mass ratios varied from 0.348 to 0.529, whereas in a walrus, with its larger 1,250 g brain, the ratio dropped to 0.151 (within the range of our delphinid values).

Tower [1954] presented evidence based on data from various mammals, including one cetacean species (*Balaenoptera physalus*), that larger brains generally feature a decrease in the density of cerebral cortical neurons. This inverse correlation mirrors the relationship between CCA/BM and BM within our delphinid study group. Since

in eutherians the corpus callosum is the major structural linkage between right and left isocortical neurons, the reduction in the corpus callosum in delphinids may signal in part a decreased density of isocortical neurons commensurate with the relatively large brain size in this group. While cortical neuron density assessments have been rarely accomplished in cetaceans, and the distinctions between primary and association cortex remain unclear, Morgane et al. [1988] in a study of the visual cortex in dolphins reported a total mean density of 40,000 neurons/mm³ in lateral gyrus homolaminar cortex, which had the features of primary projection or association cortex. Garey and Leuba [1986] calculated neuronal densities of 23,000 and 44,200 cells/mm³ in anterior and posterior lateral gyrus cortex, respectively, in adult Atlantic bottlenose dolphins. By comparison, Tower [1954] determined an average density of 6,800 neurons/mm³ in random cortical samples from two fin whale (*B. physalus*) brains, where brain mass was 6,500 g and 7,100 g. Since both Garey and Leuba [1986] and Morgane et al. [1988] worked with a much smaller cetacean (the bottlenose dolphin), whose brain size is similar to that of a human, the greater neuronal density in their studies follows Tower's general concept of lower densities in larger brains. Our own study hints at a qualitatively similar relationship with respect to relative callosal size and brain mass in similar species, with a ratio of 0.15 in the two balaenopterid mysticetes and mean ratios of 0.172, 0.228 and 0.272 in the Atlantic bottlenose dolphin and two stenellid species (the pantropical spotted and spinner dolphins), respectively. The regression through our ratio data presents a slope (-0.36) similar to that through Tower's (-0.32) (fig. 3). Should Tower's interpretation be correct, callosal size could then feasibly reflect cortical neuron density. However, given the regional variations cortical thickness and neuronal density, which have been observed even within a single cetacean brain, caution is best advised for the present in accepting the inverse relationship between brain size and neuron density (and the implications for corpus callosum size) in this mammal group. We suspect that Tower's concept may require some revision when more reliable data become available on a greater number of larger brains.

Despite the general correlation between BM and CCA/BM in our study sample, possible digressions from this theme need further attention as additional specimens become available. For example, while brain mass in the blue whale we cited was over twice that of the minke whale, the ratio in both brains was essentially identical (0.15). Furthermore, our examination of a single manatee brain revealed a somewhat higher ratio (0.829) than we might expect for a 302 g brain (compare the 314 g brain of

one of our California sea lions where the ratio was 0.348). In humans, sexual dichotomy in corpus callosum and brain size allometry demonstrates that variations can exist, even within a single species, that are not solely a function of brain mass: while corpus callosum midsagittal area is similar in both sexes, smaller mean brain mass in females results in a larger female ratio [de Lacoste-Utamsing and Holloway, 1982; Peters, 1988]. (In our own study, sample sizes were not generally large enough to contrast values between sexes. Only for the bottlenose dolphin did we attempt to compare 10 males and 5 females, finding no significant difference between the two groups.) Ridgway's [1986] comparison between a human brain and a killer whale brain, where encephalized mass differed between the two nearly five-fold, while corpus callosum size was similar in both, supports the possibility that factors in addition to brain size may be operating to drive the magnitude of interhemispheric connectivity via the corpus callosum.

Since the corpus callosum is the major commissural link between cerebral cortical neurons of both hemispheres, it would be desirable to relate its size more specifically to cerebral cortical neuronal mass rather than the seemingly more crude measure of brain size, since the latter additionally encompasses all fiber components and other neuronal centers deep to the cortex. Rockel et al. [1980], in a study that included selected primates, rodents and carnivores, determined that the number of neurons in a column of cerebral cortex was similar (with the exception of the striate visual cortex in primates), regardless of cortical thickness, as neuronal densities shifted inversely with cortical depth. Should this uniformity extend to cetaceans, a measure of absolute neuronal mass would directly relate to cortical surface area. However, cortical surface has been shown to vary directly with brain mass in cetaceans [Ridgway and Brownson, 1984; Jerison, 1991], and such determinations would accordingly offer no advantages over CCA/BM since neuronal mass would then vary directly with brain mass as well. Garey and Leuba [1986] countered on the basis of their density counts in the bottlenose dolphin, however, that the generality proposed for mammals by Rockel et al. [1980] might not necessarily apply to dolphins. If cetaceans are unique in this regard, it would then be necessary to determine specific neuronal densities and correlate them with cortical thickness in order to quantify cortical neuronal mass in this group. While estimates of neuronal density in the visual cortex of the bottlenose dolphin have been provided by Garey and Leuba [1986] and Morgane et al. [1988] on paraffin and celloidin embedded materials, respectively, interpretations of absolute counts are complicated by shrinkage artifact which accompanies these pro-

cessing methods [O'Kusky and Colonnier, 1982; Schüz and Palm, 1989]. In addition, cortical thickness has been shown to vary with cetacean species and not necessarily in direct proportion to brain size [Pilleri and Kraus, 1969]. Until additional data on neuronal density and cortical thickness are available across a range of cetacean species (or it can be determined that the cortical uniformity presented by Rockel et al. holds for cetaceans), it will be difficult to specifically relate neuronal mass to such brain parameters as the corpus callosum area.

Phylogenetic separation between the cetaceans and terrestrial mammals over at least the past 55 million years [Gingerich et al., 1983] has reasonably offered opportunities for the operation of niche-specific selective pressures during a time when both marine and land-based mammals were independently undergoing a process of encephalization [Jerison, 1973]. Many investigators have discussed the significance of the corpus callosum for interhemispheric communication in support of cerebral lateralization of higher cortical functions in humans [Myers and Sperry, 1953; Myers, 1956, 1959; Sperry, 1961, 1962, 1982; Gazzaniga, 1966; Bogen, 1969; Witelson, 1985, 1986; O'Kusky et al., 1988; Peters, 1988]. The utility of the commissural systems in the coordination of sensorimotor functions (e.g., those involving sight or sound) has also received attention in humans, other primates and other terrestrial mammals [Berlucchi, 1978; Garey, 1979; Innocenti, 1979, 1986; Weiskrantz, 1979]. Yet the potential for some fundamental mechanistic distinctions in the cetacean order must be considered from findings in such species as the bottlenose dolphin, where the cerebral hemispheres have independently produced (during simultaneous recordings), electroencephalograph waveforms indicative of wakefulness (low voltage, fast activity) in one hemisphere while the opposite hemisphere appears to sleep (high voltage, slow wave) [Mukhametov et al., 1977; Mukhametov, 1984]. Evolutionary pressures favoring hemispheric independence (for whatever reasons) may have diminished the need for some

aspects of the communicative link between hemispheres necessary to other mammals, while leaving other expressions of cetacean encephalization unchecked. Thus, while in such highly lateralized mammals as humans, where interhemispheric coordination sustains an elaborate functional asymmetry, we might expect a larger commissural link relative to brain mass than in other mammals (e.g., cetaceans) where cerebral independence may be favored over needs of lateralization and commissural development.

Finally, the degree of connectivity indexed by the midsagittal area of the corpus callosum within the cetacean group itself must be further explored by considering neuron fiber size and density across the midsagittal bridge. Lamentia and Rakic [1990] have noted in their study of cerebral commissures in the rhesus monkey that regional variations of axonal size and density in the midsagittal plane frustrate the rigor of macroscopic commissural area measurements in predicting the number of axons conveyed through the commissure. Given such regional variations within a single species, we might reasonably suspect mean differences in axonal size and numbers between species, especially perhaps within such mammalian families as the delphinids, where brain mass itself varies through a broad range. Information addressing callosal fiber density in cetaceans will need to be assembled before the power of midsagittal size in defining the communicative link provided by the corpus callosum can be more accurately assessed.

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